

Habitat use in an assemblage of Central American wandering spiders

Witold Lapinski¹ and Marco Tschapka^{1,2}: ¹Institute of Experimental Ecology, University of Ulm, Albert-Einstein-Allee 11, 89069 Ulm, Germany. E-mail: witold.lapinski@uni-ulm.de; ²Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa Ancón, República de Panamá

Abstract. The sympatric occurrence of species is thought to be based mainly on the differences in their use of habitat and of limiting resources. Segregating parameters may be of spatial or temporal character and may include behavioral differences. We hypothesized that species of large hunting spider living sympatrically in a Costa Rican lowland rain forest should differ in their habitat and/or hunting microhabitat preferences, in daily activity pattern, and, as an adaptation to the preferred hunting microhabitat, in their specific ability to adhere to smooth surfaces. We found an assemblage of eight large species of the families Ctenidae and Trechaleidae, consisting of three subguilds: 1) two semi-aquatic species with low adhesion ability, 2) three forest-floor dwelling species with good adhesion ability, and 3) three vegetation dwelling species showing very good adhesion ability. The species were partially segregated by habitat type, with two of the vegetation dwelling species preferring the treeless area of a temporary swamp. We found no species-specific differences in daily activity patterns. The similarity in community structure between this Costa Rican and a central Amazonian assemblage suggests the existence of similar structuring mechanisms in wandering spider assemblages in climatically similar biomes.

Keywords: Coexistence, habitat preference, natural prey, niche, sympatry, Ctenidae, Trechaleidae

Niche theory suggests that coexistence of similar species is based on differences that allow a species-specific use of limited resources, thus avoiding or diminishing competition within animal communities (Putman 1994). Such differences may also be based on spatial (or temporal) aspects: spiders not only can use different ways to capture prey, but also can hunt in different places (or at different times) for the same type of prey in a similar way. As abundant and mostly unspecialized predators, spiders are important elements of many terrestrial animal communities (Wise 1993; Pfeiffer 1996; Hurtado Guerrero et al. 2003; Sørensen 2003). Wandering spiders, specifically spiders not using webs for prey capture and therefore having low site fidelity, may have high population densities and a considerable impact on arthropod communities (Wise 1993; Sørensen 2003). Although many tropical habitats harbor many of these species, they are rarely studied.

Local assemblages may be composed of several large species that on first glance appear to be quite similar to each other in morphology and hunting behavior. However, similar sympatric species frequently differ in microhabitat and diet preferences and, less frequently, also in temporal activity patterns (e.g., Mühlenberg 1993; Moring & Stewart 1994; Menin et al. 2005). Nevertheless, niche width may overlap to some extent (Putman 1994), especially when considering largely unspecialized predators such as spiders. To assess the community ecology of large araneomorph wandering spiders, we studied patterns of habitat segregation within a Costa Rican lowland forest assemblage composed of similarly sized species of the families Ctenidae and Trechaleidae.

The pantropically distributed Ctenidae family (superfamily Ctenoidea: Silva Davila 2003) contains some of the largest araneomorph wandering spider species, with body lengths of more than 4 cm. In tropical lowland habitats, these spiders are often found in assemblages consisting of several large species. Frequently, these large spiders occur sympatrically

with the New World endemic family Trechaleidae (superfamily Lycosoidea: Silva Davila 2003) that contains species of similar size to the Ctenidae (Carico 1993). Although some studies have focused on various aspects of selected tropical wandering spider taxa (Van Berkum 1982; Barth et al. 1988; Carico et al. 1985; Schmitt et al. 1990; Carico 1993; Höfer et al. 1994; Gasnier & Höfer 2001; Steyn et al. 2002; Dias & Brescovit 2004; Torres-Sánchez & Gasnier 2010), no studies on community patterns within assemblages of similarly sized sympatric species belonging to different families are yet available. Consequently, our goal was to make an ecological analysis of an assemblage of large wandering spider species. We quantified habitat parameters in order to assess patterns of habitat use. We hypothesized that species should differ from each other in habitat and/or microhabitat choice, and that species with preferences for different microhabitats should also differ in their ability to adhere to smooth surfaces. Plant dwellers should have better adhesive abilities than ground dwellers because they often move on vertical surfaces and on the undersides of smooth leaves. Additionally, we expected different diurnal activity patterns of the species.

METHODS

Study site.—We conducted field work at the Reserva Biológica Tirimbina (RBT; 10°24'N, 84°07'W, 180–220 m asl), Heredia Province, Costa Rica, comprising an area of 345 ha adjacent to the Sarapiquí River. Mean annual temperature is 25.3°C and mean annual precipitation is 3777 mm. Near the Sarapiquí River lies a temporary swamp that is partly covered by forest; however, its main area lacks trees and is densely covered with tall (up to 3.5 m) grass, vines, *Heliconia* spp. (Heliconiaceae) and Maranthaceae up to 6 m tall. RBT includes areas belonging to two life zones: very humid, tropical, pre-montane forest and transitional very humid tropical forest (Holdridge 1967). Eighty-five per cent of

the reserve's forest is classified as "primary forest." RBT also encompasses areas of secondary forest of various age classes and an abandoned cacao plantation with relatively short (ca. 6–10 m) cacao trees, with some taller shade trees and very little undergrowth, surrounded by forest (Reserva Biológica Tirimbina 2009).

Sampling.—To obtain data on habitats and hunting microhabitats, we searched for active subadult and adult spiders over the course of 50 nights, from 1830 h to 0550 h (22 April to 10 July 2008). All spiders encountered at the entrance or outside of their day shelters were considered to be active. Only large species with a body length ≥ 17 mm were surveyed. We identified species using the literature available (Pickard-Cambridge 1897, 1897–1905; Carieo 1993; Höfer & Breseovit 2000; Barth 2001; Simó & Brescovit 2001). Voucher specimens were preserved in ethanol (70%) and deposited in the Museo de Zoología, Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica.

Habitat, hunting microhabitat and activity: We conducted most of the fieldwork in the western part of RBT along trails, two creeks, two canopy bridges (height = 0–24 m) and within a temporary swamp. Although the canopy bridges allowed us to detect spiders up to 30 meters above ground, most individuals on higher tree trunks and branches could not be reached. We obtained the majority of the data from the forest floor and the understory. Spiders were marked individually on the carapace with small, numbered, plastic tags used in beekeeping in order to avoid repeated sampling. We attached the tags to the carapace by non-water-soluble Tippex™ (modified after Azevedo 1999). Date and time of each encounter were recorded. We distinguished the following habitat types: forest, gap, forest margin, temporary swamp (treeless part), and cacao plantation.

In order to characterize hunting microhabitat preferences, we recorded the following parameters for each individual: type of hunting microhabitat (with the classes: st = stone, so = soil, wa = water, lo = log, vr = vines and thin hanging roots, br = branch, le = leaf, pest = petiole of a leaf of a palm/stem of a tall grass, tru = tree trunk), height above ground (HG, in m), distance to the nearest water body (DW, in m), temperature close to the spider (T, in °C, precision 0.1°C), and angle of inclination of the substrate it sits on (α , in degrees °C). We also recorded degree of cover (DC) by epiphylls, grass or leaf litter around an individual, as it can provide shelter or obstruct the locomotion of relatively small animals such as spiders, thus altering the preferred surface structure among species. We estimated the degree of cover around an individual spider using a transparent plastic sheet of 58 × 40 cm with a grid of 2 × 2 cm squares. Height of cover around the spider (HC, in cm) was scored as the mean of six measurements: four in a distance of 10 and 20 cm in front of and behind the spider, respectively, and two 10 cm to the right and the left of the spider.

Prey: Whenever one of our focus species encountered a prey item, we tried to identify it at least to ordinal level. The aim was to verify an overlap of diet among the spider species studied. Body mass of prey was recorded using a digital portable balance (Acculab, Sartorius Group, Pocket Pro-PP 62, accuracy 0.01 g). As prey data were scarce during

Table 1.—Co-occurring species of large wandering spiders within RBT. The numbers of individuals for each gender include both subadults and adults, except that for *P. boliviensis*, two females of a stage prior to the subadult stage were included.

Species	Females	Males	Sum
<i>Ancylometes bogotensis</i> (Keyserling 1877)	13	9	22
<i>Phoneutria boliviensis</i> (F.O.P.-Cambridge 1897)	3	3	6
<i>Cupiennius coccineus</i> F.O.P.-Cambridge 1901	43	23	66
<i>Cupiennius getazi</i> Simon 1891	12	10	22
<i>Ctenus sinuatipes</i> F.O.P.-Cambridge 1897	17	6	23
<i>Ctenus curvipes</i> (Keyserling 1881)*	13	7	20
<i>Ctenus</i> sp. 3	19	14	33
<i>Trechalea tirimbina</i> Silva & Lapinski 2012	14	13	27
Total	134	85	219

* New species record for Costa Rica.

fieldwork in 2008 ($n = 37$), we added data collected between July 2010 and March 2012.

Adhesion ability and body mass: The animals' ability to adhere to smooth surfaces such as leaves was experimentally quantified in order to assess whether it corresponded to the surface of the preferred hunting microhabitat. We used plexiglass as a standardized smooth surface in order to test the individuals under constant and reproducible conditions. Each spider was placed on a plexiglass square (20 cm × 20 cm). The angle of inclination (β) of this square was then slowly increased in steps of 45°, so that the position of the spider changed from being on the upper side (0 and 45°), to hanging on a vertical surface (90°), to finally clinging to the underside of the plexiglass (135 and 180°). The largest angle at which the spider was still able to stay attached to the plexiglass was recorded. Body mass of each spider (m) was assessed using a portable digital balance (see above).

Statistical analyses.—In order to show the overall assemblage pattern and the position of microhabitat variables and adhesion ability relative to each other and to the centroids of the species, we conducted an unrotated Principal Component Analysis (PCA) using Statistica (Version 6.0). The data were $\log_{10}(x+1)$ -transformed and standardized. For each microhabitat type, we used presence/absence data of each spider species, the mean values of HG, DW, T, α , DC and HC measured near the spiders and of β of the spiders in the respective microhabitat type (see above). We then used SigmaStat (Version 3.5) to test for interspecific significant differences. We tested for interspecific differences in use of microhabitat classes (nominal variables) with a Chi-square test. For continuous variables, analysis of variance (ANOVA) was applied to normally distributed and Kruskal-Wallis ANOVA to non-normally distributed data. Dunn's method was used as a post-hoc test, to compare data that were not normally distributed and were of unequal size.

RESULTS

Species composition.—We found 219 large spiders belonging to seven species of the family Ctenidae and one species of the family Trechaleidae (Table 1). Median body mass of female

Table 2.—Prey of the spider species studied. Species abbreviations: Ab = *Ancylometes bogotensis*, Cc = *Cupiennius coccineus*, Cg = *Cupiennius getazi*, Cts = *Ctenus sinuatipes*, Ctc = *Ctenus curvipes*, Ct 3 = *Ctenus* sp. 3, Pb = *Phoneutria boliviensis*, Tt = *Trechalea tirimbina*.

Prey	Predators							
	Ab	Cc	Cg	Ctc	Cts	Ct 3	Pb	Tt
Arachnida								
Amblypygi						1		
Araeneae	1	3	2		1	1	3	4
Opiliones		1		1				
Scorpiones		1						
Insecta								
Blattodea				2				
Dermaptera		1						
Heteroptera			1					
Homoptera		1			1			
Hymenoptera							1	
Lepidoptera		1						
Odonata			1					
Orthoptera		5	2	1	2		2	4
Phasmida		1						
Scolopendromorpha								
				1	1	1		
Vertebrata								
Anura		1		1				
Cyprinodontiformes	1							
Squamata				1				
Totals	2	15	6	7	5	3	6	8

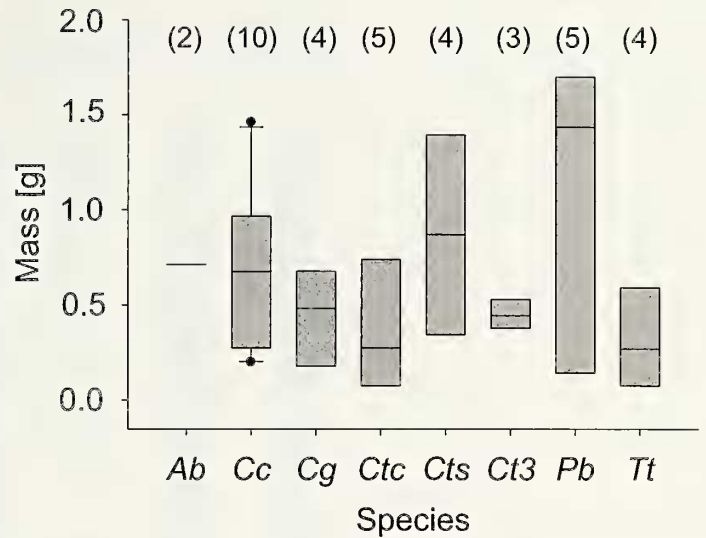


Figure 1.—Box plot of mass of prey items captured by the spider species. For species abbreviations see legend to Table 2. Numbers in brackets indicate sample size.

spiders ranged between 0.68 g [*Ctenus curvipes* (Keyserling 1881)] and 2.59 g [*Ancylometes bogotensis* (Keyserling 1877)]; males ranged between 0.73 g (*Ct. curvipes*) and 2.31 g [*Phoneutria boliviensis* (F.O.P.-Cambridge 1897)]. No other araneomorph wandering spider species of similar size were observed at the study site.

Prey.—During both field trips, we observed spiders with prey that could be identified at least to ordinal level in 52 cases. Seventeen taxa (suborder or order) were observed as prey of the spiders, including three vertebrate orders. Other spiders (Araneae) and orthopterans (mainly crickets and katydids) were consumed by most of the spider species studied (Table 2). During our first field trip, the body mass of the prey items ($n = 37$) did not differ significantly among the spider species (Fig. 1; ANOVA: $F_{7,29} = 1.2, P = 0.32$).

Overall assemblage structure.—The PCA of the presence/absence data of the spider species, hunting microhabitat types, and adhesion ability shows a structured assemblage (Fig. 2). The eigenvalues were 4.06 (1st axis) and 1.68 (2nd axis). These two principal components explained 81.9% of the total variance in the data set.

The PCA suggested that the presence of *A. bogotensis* and *Trechalea tirimbina* Silva & Lapinski 2012 was negatively correlated with distance to a water body (DW), height above ground (HG), degree of cover (DC), and height of cover (HC). These species appear to be associated with the microhabitat types of water, stone, log, and vines and thin hanging roots. The presence of the three *Ctenus* species appeared to be positively correlated with the temperature of the hunting

microhabitat (T), DC and HC, and DW (less so for *Ctenus* sp. 3), but negatively correlated with α . Those species appear to be associated with the following microhabitat types: soil, tree trunk, and branch. PCA suggested a positive correlation of the presence of *Cupiennius coccineus* F.O.P.-Cambridge 1901 with DW, HG, and an association with the microhabitat types of tree trunk, branch and leaf. Presence of *Cupiennius getazi* Simon 1891 and *P. boliviensis* appeared to be positively correlated with α and HG, and negatively with T, DC and HC. The analysis suggested an association of those species with the

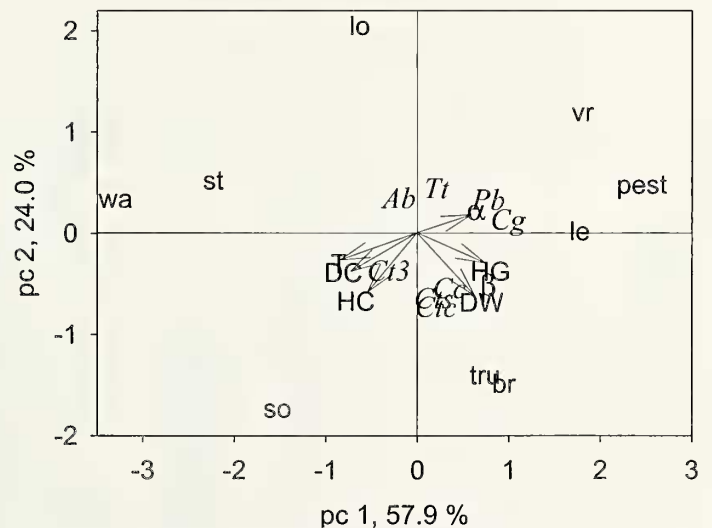


Figure 2.—Principal component analysis (PCA) biplot showing the overall assemblage structure at RBT. Abbreviations: st = stone, so = soil, wa = water, lo = log, vr = vines and thin hanging roots, br = branch, le = leaf, pest = petiole of a leaf of a palm/ stem of a tall grass, tru = tree trunk, HG = height above ground, DW = distance to the nearest water body, T = temperature close to the spider individual, α = inclination of the substrate a spider perches on, DC = degree of cover, HC = height of cover, β = angle of the plexiglass square, i.e. adhesion ability. For species abbreviations see legend in Table 2.

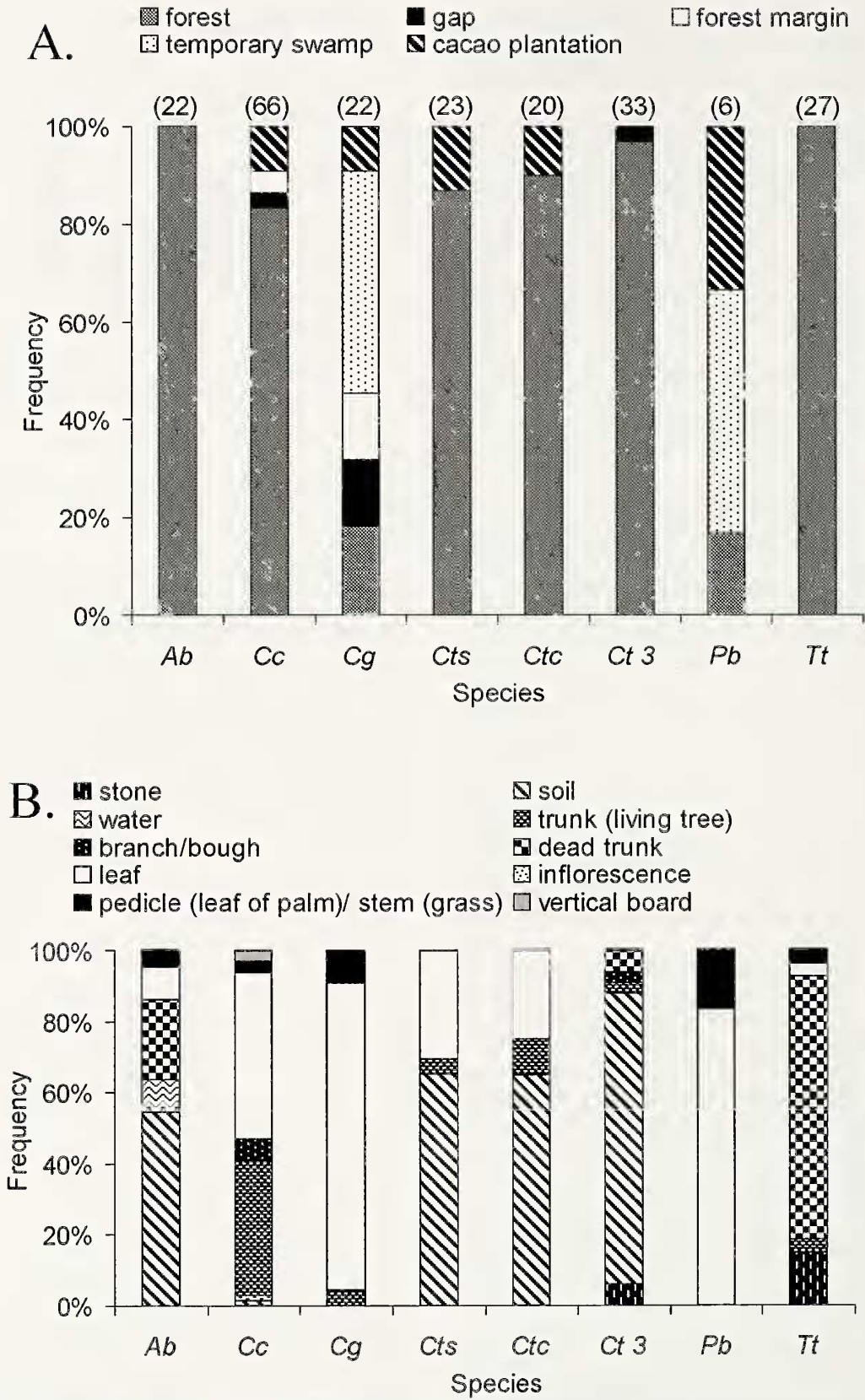


Figure 3.—Relative frequency of occurrence of the spider species at (A) habitat types and at (B) hunting microhabitats. Numbers in brackets indicate sample size. For species abbreviations, see legend in Table 2.

microhabitat types of vines and thin hanging roots, petiole of a leaf of a palm/stem of a tall grass, and leaf.

Distribution, habitats and activity.—The species occurred in five different habitat types (Fig. 3A). Eighty-two per cent of all individuals were found within the forest. *Ancylometes bogotensis* and *T. tirimbina* were present only along creeks within the forest. *Cupiennius coccineus* and the three species of *Ctenus* were widely distributed over the entire forest and appeared less frequently in the cacao plantation. *Cupiennius getazi* and *Phoneutria boliviensis* occurred mostly in treeless areas, especially on the vegetation within and around the swamp. *Cupiennius getazi* also inhabited all other habitat types, but in very low numbers. *Cupiennius coccineus*, the most abundant species overall (Table 1), was never found in open areas. Individuals of all species were encountered outside their day shelters throughout the night, and we found no specific preferences in activity time (Kruskal–Wallis ANOVA: $H_7 = 10.0$, $P = 0.19$).

Hunting microhabitat.—The spider species differed significantly in the microhabitat type on which they were found hunting (χ^2 test: $\chi^2_{56} = 322.3$, $P < 0.001$; Fig. 3B). Many spiders frequented leaves, especially both species of *Cupiennius* and *P. boliviensis*, although *C. coccineus* mainly used trees and palms, while *C. getazi* and *P. boliviensis* were found on very high grass and on *Heliconia* sp. In contrast to these three species, *A. bogotensis* and the three *Ctenus* species were found mostly on the forest floor, and only some *Ctenus sinuatipes* F.O.P.-Cambridge 1897 and *Ct. curvipes* also hunted on leaves of the lower forest vegetation. *Trechalea tirimbina* mainly used logs and stones. The distance of the respective hunting microhabitats from water (DW) differed significantly among the species, with *A. bogotensis* and *T. tirimbina* almost always occurring in the immediate vicinity of creeks and small rivers. *Ctenus* sp. 3 was also found very often near bodies of water (Kruskal–Wallis ANOVA: $H_7 = 103.2$, $P < 0.001$; Dunn's post-hoc test: $P < 0.05$; Fig. 4A). Heights above ground of the hunting microhabitats differed significantly between the spider species (Kruskal–Wallis ANOVA: $H_7 = 153.7$, $P < 0.001$; Dunn's post-hoc test: $P < 0.05$; Fig. 4B). The two *Cupiennius* species and *P. boliviensis* occurred mainly higher above the ground than the other ctenids and *T. tirimbina*.

Surface cover near the spiders on plants, logs, and rocks in the creeks consisted mainly of small epiphytes. On soil, it was predominantly composed of litter and smaller plants. Low to very low DC and HC values were found near the two *Cupiennius* species, *P. boliviensis* (in all three species: median DC = 0%, median HC = 0.0 cm), and *T. tirimbina* (median DC = 15%, median HC = 0.1 cm). High DC and HC values were found for hunting microhabitats of *A. bogotensis* and *Ctenus* sp. 3 (median DC: 40 and 39%, median HC: 1.6 and 2.2 cm, respectively). Very high DC and HC values mainly occurred in microhabitats of *Ctenus sinuatipes* and *Ct. curvipes* (median DC: 80 and 79%, median HC: 2.2 and 2.8 cm, respectively). Both parameters in the latter four species were very variable (DC = 0–100%, HC = 0.0–12.0 cm). *Ctenus sinuatipes* and *Ct. curvipes* were found in microhabitats with significantly higher DC values than the two *Cupiennius* species and *P. boliviensis*. *Ctenus curvipes* and *Ctenus* sp. 3 preferred significantly higher HC values than the two *Cupiennius* species and *P. boliviensis*. *Trechalea tirimbina* hunted in microhabitats

with significantly lower HC values than *Ctenus* sp. 3. (Kruskal–Wallis ANOVA: $H_7 = 55.7$ for DC and $H_7 = 77.3$ for HC, $P = 0.001$; Dunn's post-hoc test: $P < 0.05$; Fig. 4C–D). Temperature near individual spiders did not differ significantly among species (Kruskal–Wallis ANOVA: $H_7 = 10.6$, $P = 0.16$; Fig. 4E).

Adhesion ability.—The PCA suggested a positive correlation of β with DW and HG and proved to be characteristic for species having high HG- and/or DW- values (Fig. 2). *Ancylometes bogotensis* and *T. tirimbina* had significantly lower adhesion ability than the other species. Although these species barely reached values of 45° in the adhesion experiments, some of the others were able to cling to the plexiglass even when turned upside down ($\beta = 180^\circ$) (Kruskal–Wallis ANOVA: $H_7 = 131.7$, $P < 0.001$; Dunn's post-hoc test: $P < 0.05$; Fig. 4F).

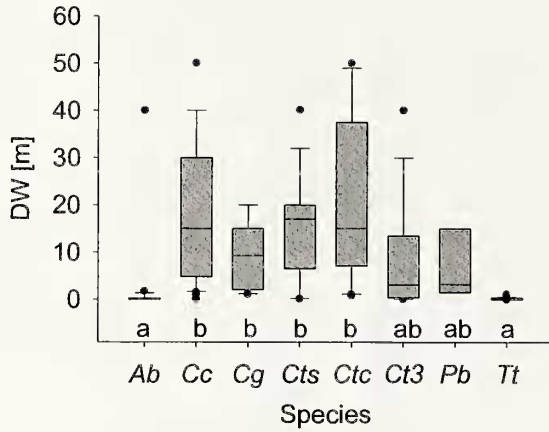
DISCUSSION

We have presented a comparative study of the ecology of an assemblage of large tropical araneomorph wandering spiders comprising two families, Ctenidae and Trechaleidae. Subadults and adults of the different species preyed on a similarly sized group of animals. Even the smallest and lightest species, *Ctenus curvipes*, was found with prey of considerable body mass that overlapped widely with the prey of all other species. Although data on prey are limited, we conclude that the large wandering spiders at the study site form an ecological guild, defined by the use of the same resources (Root 1967). However, our data also show that the eight species are almost entirely segregated by different habitat use, and within overlapping habitat sections they differed in microhabitat choice.

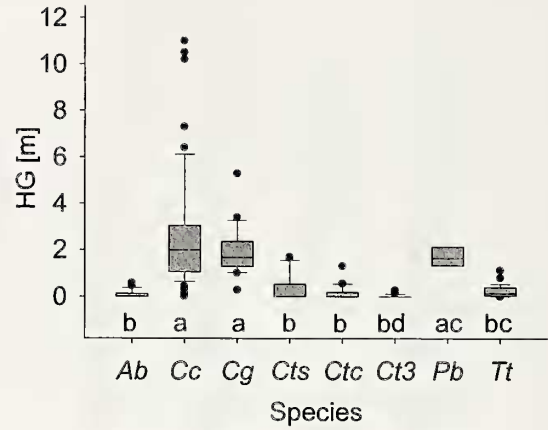
Habitat segregation was most noticeable for *C. getazi* and *P. boliviensis*, with a preference for treeless habitats. The presence of *C. getazi* and the absence of *C. coccineus* from such habitats were also reported by Schuster et al. (1994). The close proximity to water of *A. bogotensis* and *T. tirimbina* corroborates the reported strong association of these two genera with water (Carico 1993; Höfer & Brescovit 2000), separating them from the other six species.

Contrary to our expectation, all species were found throughout the night. This confirms the lack of temporal separation reported for four *Ctenus* species from central Amazonia (Gasnier 1996). Schmitt et al. (1990) found constant activity of *C. coccineus* over the whole night and a high activity of *C. getazi* during the first half of the night. Although nightly movements of individuals were not included in the scope of this study, no species-specific hunting times could be detected in the field. In tropical regions with weakly pronounced seasons as in RBT, the abundance of subadult and adult spiders is relatively low (Russell-Smith & Stork 1995; Silva 1996; Rego et al. 2005). The relatively low abundance of potential intraguild competitors, together with the spatial segregation of the species, makes it plausible that no species-specific nighttime preferences have developed. Considering the spiders' low-cost sit-and-wait predatory strategy, no significant saving of energy could be achieved by hunting for only part of the night, reducing potential hunting success even more. Temperature near the spiders does not seem to be an important variable for hunting microhabitat

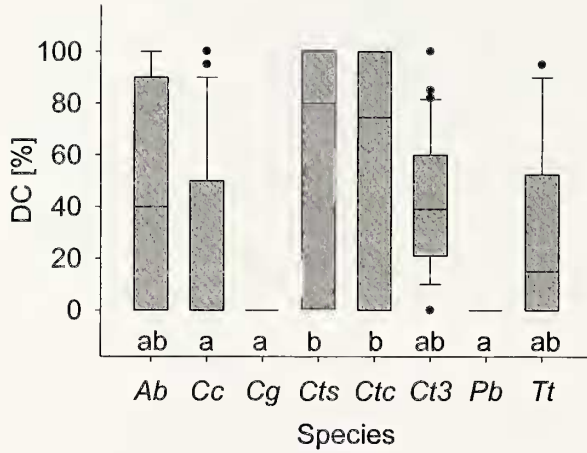
A.



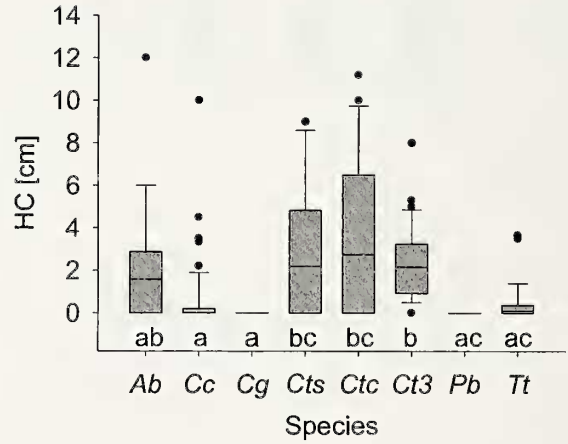
B.



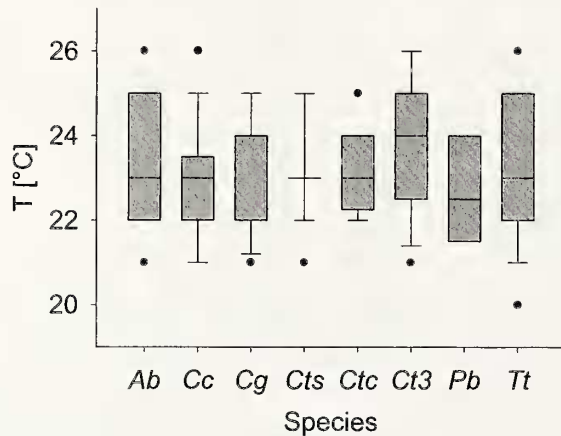
C.



D.



E.



F.

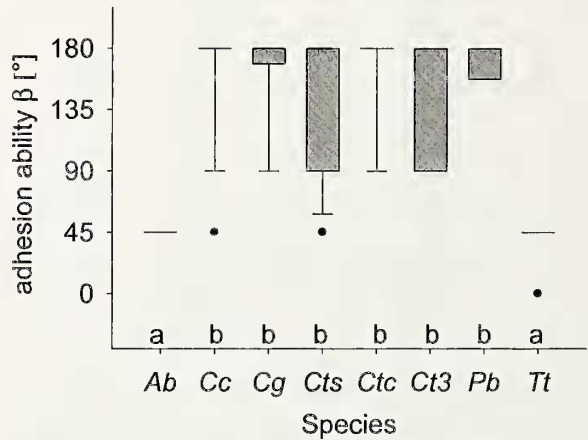


Figure 4.—Comparison of variables of the microhabitats and adhesion ability of the wandering spiders. Distance from the next water body (A), height above ground (B), degree of cover (C), height of cover (D), temperature (E), and achieved maximum angle of inclination in the adhesion tests (F). Different letters below box plots indicate significant differences based on Dunn's post hoc test. For species abbreviations see legend in Table 2.

choice, which probably mirrors the relative microclimatic homogeneity of the RBT forest.

Our findings on habitat separation are consistent with previously published results on vertical segregation in other generalized predators of arthropods, such as *Anolis* lizards (Reagan 1992), hylid frogs (Menin et al. 2005), and *Norops* lizards (D'Cruze & Stafford 2006). Among arthropods, generalist predators are mainly constrained by their tolerance for environmental conditions of the strata (Basset et al. 2003). In tropical Africa, most species of Ctenidae occurred on the forest floor and in the understory, with none in the canopy (> 3.0 m above ground) (Steyn et al. 2002; Sørensen 2003). In those forests, ctenids might be replaced in the higher forest strata by species of other wandering spider families. Unfortunately those studies were restricted only to ctenids. In the Amazon, *Phoneutria reidyi* (F.O.P.-Cambridge 1897) was also found on vegetation up to 5 m above ground (Torres-Sánchez 2000; Torres-Sánchez & Gasnier 2010). The total height range used by the RBT wandering spiders, especially *C. coccineus*, was probably underestimated because most data could only be obtained by observation from the ground. Using adequate canopy access techniques should resolve that question. Our results indicate, however, that large ctenids frequently do occur at greater heights above ground.

The wide ranges in degree and height of cover in the microhabitats hunted by most of the species probably mainly reflects the conditions within the respective habitats. Thus, leaf litter appears to be an important factor for the three *Ctenus* species, but is less so for the other species. In other wandering spider assemblages, microhabitats may differ in depth or complexity of leaf litter (Uetz 1977; Gasnier 1996). The amount and complexity of leaf litter is considered to affect hunters as well as potential prey organisms by providing protection from different abiotic impacts, but also by offering shelter from predators (Fauth et al. 1989; Wise 1993).

We confirmed our hypothesis that the hunting microhabitat preferences of the sympatric wandering spider species would also be reflected by their specific ability to adhere to smooth surfaces. Although adhesion abilities are probably of little importance in the semi-aquatic microhabitats of *T. tirimbina* and *A. bogotensis*, this quality plays a more important role in vegetation dwellers. Due to their high adhesion ability, the three *Ctenus* spp. seem to be preadapted to a broad range of microhabitats, including the forest floor and also the higher vegetation. The high adhesion abilities of the vegetation dwellers (*Cupiennius* spp. and *P. boliviensis*) might be particularly advantageous when climbing on smooth surfaces, even on the undersides of leaves in head-down position.

Based on our results, the eight large wandering spider species of RBT can be assigned to three main subguilds:

- 1) **Semi-aquatic species** (sensu Graham et al. 2003): *Ancylometes bogotensis* and *Trechalea tirimbina* are strongly associated with water bodies and have poor adhesion abilities.
- 2) **Ground-dwelling species**: Three *Ctenus* spp. forage on the forest floor and hide among the debris and have good adhesive capabilities.
- 3) **Vegetation-dwelling species**: These species are strongly associated with vegetation and have very good adhesive capabilities: two *Cupiennius* species and *Phoneutria*

boliviensis. *Cupiennius coccineus* prefers forest sites, while *C. getazi* and *P. boliviensis* are habitat generalists that may prefer treeless areas.

Our results on the wandering spiders agree with studies that show species-specific habitat preferences within different taxa of animals; e.g., assemblages of frogs, lizards, and spiders (Uetz 1977; Reagan 1992; Dias & Brescovit 2004; Menin et al. 2005; D'Cruze & Stafford 2006; Williams et al. 2006; Entling et al. 2007; Torres-Sánchez & Gasnier 2010).

The only site where large tropical wandering spiders have been studied in some detail is the Reserva Florestal Adolpho Ducke (RFAD) in central Amazonia, Brazil. *Ancylometes* species were frequently found on the ground near water (Azevedo 1999; Höfer & Brescovit 2000), *Ctenus* species lived mainly on the forest floor but also climbed into the lower vegetation stratum (Höfer et al. 1994; Gasnier 1996), and two *Phoneutria* species dwelled on the forest floor and on plants (Torres-Sánchez 2000; Simó & Brescovit 2001; Torres-Sánchez & Gasnier 2010). Habitat use within the local wandering spider assemblage therefore seems to be rather similar in RBT and in RFAD. The similarity of these two neotropical assemblages suggests that similar microhabitats and selection pressures have led to similar abilities and lifestyles of the species at both sites. Consequently, we expect similarity at the structural level, but not necessarily at the taxonomic level, among wandering spider assemblages of different geographical regions with similar climatic conditions.

In conclusion, the assemblage of sympatric wandering spiders at the Reserva Biológica Tirimbina showed a clear structure, and the species differed clearly in habitat and hunting microhabitat selection. This points to the importance of habitat heterogeneity for species coexistence. These ecological preferences were correlated with abilities to adhere to certain microhabitat surfaces. Our data suggest the existence of assembly mechanisms for large hunting spiders that are based primarily on structural habitat parameters.

ACKNOWLEDGMENTS

We thank the German Academic Exchange Service (DAAD) for a scholarship supporting fieldwork of WL in Costa Rica. Hubert Höfer (State Museum of Natural History, Karlsruhe, Germany) provided us with valuable unpublished Masters and Doctoral theses. M. Pfeiffer (University of Ulm, Germany) helped with the multivariate statistical analysis. The MINAET (Ministerio de Ambiente, Energía y Telecomunicaciones, Costa Rica) kindly gave us the permit to conduct field work in Costa Rica. The friendly assistance of Javier Guevara (MINAET) is greatly appreciated. We are very grateful to Bernal Rodríguez-Herrera (RBT and UCR) and all staff members at the Reserva Biológica Tirimbina for all their friendliness and support, and for allowing us to complete this project at the station.

LITERATURE CITED

- Azevedo, C.S. 1999. Ecologia de *Ancylometes gigas* (Pickard-Cambridge, 1897) (Araneae: Pisauridae), uma aranha errante que vive próximo a corpos de água em uma floresta tropical úmida. M.Sc. Dissertation. UA/INPA/CAPES. Manaus, Brazil.
- Barth, F.G. 2001. Sinne und Verhalten: aus dem Leben einer Spinne. Springer-Verlag, Berlin.

- Barth, F.G., E.A. Seyfarth, H. Bleckmann & W. Schüch. 1988. Spiders of the genus *Cupiennius* Simon 1891 (Araneae, Ctenidae). I. Range distribution, dwelling plants, and climatic characteristics of the habitats. *Oecologia* 77:187–193.
- Basset, Y., P.M. Hammond, H. Barrios, J.D. Holloway & S.E. Miller. 2003. Vertical stratification of arthropod assemblages. Pp. 17–27. *In* *Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy*. (Y. Basset, V. Novotny, S.E. Miller & R.L. Kitching, eds.). Cambridge University Press, New York.
- Carico, J.E. 1993. Revision of the genus *Trechalea* Thorell (Araneae, Trechaleidae) with a review of the taxonomy of the Trechaleidae and Pisauridae of the Western Hemisphere. *Journal of Arachnology* 21:226–257.
- Carico, J.E., J. Adis & N.D. Penny. 1985. A new species of *Trechalea* (Pisauridae: Araneae) from Central Amazonian inundation forests and notes on its natural history and ecology. *Bulletin of the British Arachnological Society* 6:289–294.
- D’Cruze, N.C. & P.J. Stafford. 2006. Resource partitioning of sympatric *Norops* (beta *Anolis*) in a subtropical mainland community. *Herpetological Journal* 16:273–280.
- Dias, S.C. & A.D. Brescovit. 2004. Microhabitat selection and occurrence of *Pachistopelma rufonigrum* Pocock (Araneae, Theraphosidae) and *Nothroctenus fixico* sp. nov. (Araneae, Ctenidae) in tank bromeliads from Serra de Itabaiana, Sergipe, Brazil. *Revista Brasileira de Zoologia* 21:789–796.
- Entling, W., M.H. Schmidt, S. Bacher, R. Brandl & W. Nentwig. 2007. Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. *Global Ecology and Biogeography* 16:440–448.
- Fauth, J.E., B.J. Crother & J.B. Slowinsky. 1989. Elevational patterns of species richness, evenness, and abundance of the Costa Rican leaf-litter herpetofauna. *Biotropica* 21:178–185.
- Gasnier, T.R. 1996. Ecologia comparada de quatro espécies de aranhas errantes de gênero *Ctenus* (Walckenaer) (Araneae, Ctenidae) em uma floresta na Amazônia Central: Bases para um modelo integrado de coexistência. Dr. Dissertation, UA/INPA/CAPES. Manaus, Brazil.
- Gasnier, T.R. & H. Höfer. 2001. Patterns of abundance of four species of wandering spiders (Ctenidae, *Ctenus*) in a forest in central Amazonia. *Journal of Arachnology* 29:95–103.
- Graham, A.K., C.M. Buddle & J.R. Spence. 2003. Habitat affinities of spiders living near a freshwater pond. *Journal of Arachnology* 31:78–89.
- Höfer, H. & A.D. Brescovit. 2000. A revision of the Neotropical spider genus *Ancylometes* Bertkau (Araneae: Pisauridae). *Insect Systematics and Evolution* 31:323–360.
- Höfer, H., A.D. Brescovit & T.R. Gasnier. 1994. The wandering spiders of the genus *Ctenus* (Ctenidae: Araneae) of Reserva Adolfo Ducke, a rainforest reserve in central Amazonia. *Andrias* 13:81–98.
- Holdridge, L.R. 1967. *Life Zone Ecology*. San José, Costa Rica: Tropical Science Center.
- Hurtado Guerrero, J.C., C.R. Vasconcelos da Fonseca, P.M. Hammond & N.E. Stork. 2003. Seasonal variation of canopy arthropods in Central Amazonia. Pp. 170–175. *In* *Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy*. (Y. Basset, V. Novotny, S.E. Miller & R.L. Kitching, eds.). Cambridge University Press, New York.
- Menin, M., D. De Rossa-Feres & A. Giaretta. 2005. Resource and coexistence of two syntopic hylid frogs (Anura, Hylidae). *Revista Brasileira de Zoologia* 22:61–72.
- Moring, B.J. & K.W. Stewart. 1994. Habitat partitioning by the wolf spider (Araneae, Lycosidae) guild in streamside and riparian vegetation zones of the Conejos River, Colorado. *Journal of Arachnology* 22:205–217.
- Mühlenberg, M. 1993. *Freilandökologie*. Quelle und Meyer Heidelberg, Wiesbaden, Germany.
- Pfeiffer, W.J. 1996. Arboreal arachnids. Pp. 248–271. *In* *The Food Web of a Tropical Rain Forest*. (Reagan, D.B. & R.B. Wayne, eds.). University of Chicago Press, Chicago.
- Pickard-Cambridge, F.O. 1897. On cteniform spiders from Lower Amazons and other regions of North and South America, with a list of all known species of these groups hitherto recorded from the New World. *Annals and Magazine of Natural History* 19(6):52–106.
- Pickard-Cambridge, F.O. 1897–1905. Arachnida: Araneida and Opiliones. *In* *Biologia Centrali Americana*. Vol. II. Godman & Salvin, London.
- Putman, R.J. 1994. *Community Ecology*. Chapman & Hall, London.
- Reagan, D.P. 1992. Congeneric species distribution and abundance in a three-dimensional habitat: the rain forest anoles of Puerto Rico. *Copeia* 1992:392–403.
- Rego, F.N.A.A., E.M. Venticinquê & A.D. Brescovit. 2005. Densidades de aranhas errantes (Ctenidae e Sparassidae, Araneae) em uma floresta fragmentada. *Biota Neotropica* 5:1–8.
- Reserva Biológica Tirimbina. 2009. What is Tirimbina? Physical Description. Online at <http://www.tirimbina.org/about-us-physical.html>
- Root, R.B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* 37:317–350.
- Russell-Smith, A. & N.E. Stork. 1995. Composition of spider communities in the canopies of rainforest trees in Borneo. *Journal of Tropical Ecology* 11:223–235.
- Schmitt, A., M. Schuster & F.G. Barth. 1990. Daily locomotor activity patterns in three species of *Cupiennius* (Araneae: Ctenidae): The males are the wandering spiders. *Journal of Arachnology* 18:249–255.
- Schuster, M., D. Baurecht, E. Mitter, A. Schmitt & F.G. Barth. 1994. Field observations on the population structure of three ctenid spiders (*Cupiennius*, Araneae, Ctenidae). *Journal of Arachnology* 22:32–38.
- Silva, D. 1996. Species composition and community structure of Peruvian rainforest spiders: A case study from a seasonally inundated forest along the Samiria river. *Revue Suisse de Zoologie hors série*, 597–610.
- Silva, E.L.C. & W. Lapinski. 2012. A new species of *Trechalea* Thorell, 1869 (Araneae: Lycosoidea: Trechaleidae: Trechaleinae) from Costa Rica, with notes on its natural history and ecology. *Zootaxa* 3563:58–64.
- Silva Davila, D. 2003. Higher-level relationships of the spider family Ctenidae (Araneae: Ctenoidea). *Bulletin of the American Museum of Natural History* 274:1–86.
- Simó, M. & A.D. Brescovit. 2001. Revision and cladistic analysis of the Neotropical spider genus *Phoneutria* Perty, 1833 (Araneae, Ctenidae), with notes on related Ctenidae. *Bulletin of the British Arachnological Society* 12:67–82.
- Sørensen, L.L. 2003. Stratification of the spider fauna in a Tanzanian forest. Pp. 92–101. *In* *Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy*. (Y. Basset, V. Novotny, S.E. Miller & R.L. Kitching, eds.). Cambridge University Press, New York.
- Steyn, T.L., J.-F. Van der Donckt & R. Jocqué. 2002. The Ctenidae (Araneae) of the rainforests in eastern Côte d’Ivoire. *Annales du Musée Royal de l’Afrique Centrale (Zoologie)* 290:129–166.
- Torres-Sánchez, M.P. 2000. Padrões espaciais de abundância, ciclo reprodutivo e variação de tamanho de adultos de *Phoneutria fera* Perty e *Phoneutria reidyi* F. O. Pickard-Cambridge (Araneae, Ctenidae) na Reserva Florestal Adolpho Ducke, Amazonas, Brasil. M.Sc. Dissertation. UA/INPA/CCNPq. Manaus, Brazil.
- Torres-Sánchez, M.P. & T.R. Gasnier. 2010. Patterns of abundance, habitat use and body size structure of *Phoneutria reidyi* and *P. fera* in a Central Amazonian rainforest. *Journal of Arachnology* 38:433–440.

- Uetz, G.W. 1977. Coexistence in a guild of wandering spiders. *Journal of Animal Ecology* 46:531–541.
- Van Berkum, F.H. 1982. Natural history of a tropical, shrimp-eating spider (Pisauridae). *Journal of Arachnology* 10:117–121.
- Williams, Y.M., S.E. Williams, R.A. Alafó, M. Waycott & C.N. Johnson. 2006. Niche breadth and geographical range: ecological compensation for geographical rarity in rainforest frogs. *Biology Letters* 2:532–535.
- Wise, D.H. 1993. *Spiders in Ecological Webs*. Cambridge University Press, Cambridge, UK.

Manuscript received 19 November 2011, revised 20 February 2013.